XVI.—*On the Irregular Form of the Flower of the* Papilionaceæ. By H. Walpers*.

The irregular form of the flower of the *Papilionaceæ* has given rise to the most varied explanations, to such an extent indeed, that the enumeration of all the opinions hitherto advanced respecting the origin of this form, which, according to the point of view in which they have been considered, differ essentially from one another, would occupy too much space to be stated here. It might consequently appear almost superfluous to increase the great number of theories advanced on this interesting subject by another; and I would on that account have held back my views, which differ from all hitherto brought forward, did I not find them to be confirmed by all the researches which I have made relative to the subject.

The pod so peculiar and so characteristic (*legumen*) belonging to the entire family of the *Leguminosæ*, must, from its disposition, be regarded as the single carpel of a five carpellary fruit. DeCandolle has already drawn attention to this, without any botanist however having hitherto made use of this fact, (proved by the pentagynous genus *Affonsea*, A. St. Hilaire,) in explanation of the irregular form of the papilionaceous flower. These five pods of *Affonsea* are arranged in a circle, so that their superior seminiferous sutures are situated innermost; the individual pods have therefore to be considered as *eccentric* from the imaginary floral axis which passes through the point of union of the margins of the pods. Of these five ovaries normally *four* become abortive, from reasons it is true unknown, and a single one only remains, although exceptional cases occur of two and three ovaries in *one* flower. This sole remaining ovarium stands eccentric from

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the imaginary floral axis, and generally has lengthwise a laterally compressed form arising from the unilateral adhesion of the ovules.

The pod of the *Leguminosæ* from its situation must always be viewed as that one of the five carpellary fruit which is furthest removed from the floral axis,—it is then the inferior ovarium in the flower which is developed, while the four superior ones prove abortive; for I have found the *flores resupinati* of the *Leguminosæ* on more accurate examination to be constantly produced by the twisting of the peduncle. This twisting it is true usually takes place in the bud state, and descriptive botany has rarely taken this into consideration.

The eccentricity of the individual ovaries from the floral axis is demonstrated not merely by the *Affonsea* which has been already mentioned, but also by those cases where several ovaries occur in one flower; thus I have observed in *Cæsalpinia digyna*, Willd., Herb. No. 8026, that the two ovaries do not stand as might be expected with their broad sides parallel with one another, but in imperfect opposition, so that on the one (the right) side, one, and on the other (the left) side, two ovaries must be supposed to have been abortive.

The calyx in all *Papilionaceæ* is composed of five sepals, corresponding to the number of petals*; these enter into the most varied cohesions *inter se*; in most cases, however, they are united at least to some extent into a tube or cup, &c. and only free at the apex. Exceedingly few cases of the calyx occurring quinquepartite to the base in the fully developed papilionaceous flower are mentioned by authors, although in the embryonal state of the bud, as Schleiden and Vogel have demonstrated in their excellent 'Beiträgen zur Entwicklungsgeschichte der Blüthentheile bei den Leguminosen,' (Nov. Act. Ac. Cæs. Leop. Carol. Nat. Cur. vol. xix. p. 1.) all the subsequently cohering parts of the flower are then free, and in the course of development these parts, still consisting of delicate parenchyma, at first cohere from intimate reciprocal pressure.

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The cause of the cohesion is correctly explained by the reciprocal pressure in the flower bud, without however contributing in any way to the explanation of the very remarkable irregularity of the flowers.

The cohering-leaved calyx, however, as well as the position of the ovarium with respect to the other floral parts, appear to furnish the best explanation of this irregularity.

From the double circle of anthers present in all decandrous *Leguminosæ*, and actually to be observed in the embryonal state of the floral bud, we obtain an explanation of the alternation of the petals and ovaries which we find realized in *Affonsea*, and indicated in the other one-podded *Leguminosæ* by the position of the ovarium between the two carinal petals. This ovarium is during the flowering period in general sessile, or merely provided with so short a petiole that it does not project out of the tubular calyx. Consequently an action on the other floral parts cannot be denied to this ovarium, as it frequently attains to a considerable size, and this action is manifested by pressure on the adjacent organs, which on that account are greatly inclined to cohesions in their still parenchymatous consistency. Since the petals in proportion to the length of the calycinal tube can generally only be designated as shortly unguiculated, nay in several genera a great portion of the *lamina* is even still situated in the calyx, the lateral petals standing nearest to the ovarium cohere at their inferior margins very frequently, where the pressure which the calyx and ovarium jointly exert is most powerful, and form the carina. This pressure is even so considerable in the genus *Jonesia*, Rxb., that the petals are from the first entirely suppressed, and further the ovarium coheres at its inferior suture through its entire length with the perianthium, as I have observed in several undescribed species of this highly instructive genus. In the *Cæsalpinieæ* there are several genera with only from 1 to 3 petals, these then constantly stand in the place of the *vexillum* and of the wings (*alæ*).—Perhaps the absence of the other petals may be deduced from hence? Direct observation can only decide this question. Yet we observe in *Tamarindus Indica*, L., at the place where the two absent petals should

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The flower of the *Leguminosæ* acquires a laterally compressed appearance from the abortion of the four superior ovaries; and I am not aware of a single case where the flower of any one of this family corresponds exactly to the scheme properly deducible for it.

The petals forming the carina are, as is well known, those standing nearest to the ovarium; and they must therefore, in the true papilionaceous flower, be those situated innermost; and indeed they always closely surround the ovarium and proceed perfectly parallel with it. The two following petals, or the wings, retain their original position, and place themselves, in consequence of the lateral compression of the entire flower, over the carinal leaves, with which, by the too great pressure and considerable development of the former (as in several *Phaseoleæ* and many *Trifolieæ*) they frequently cohere at their base, naturally however above the unguis. But they are generally prevented by the gamosepalous calyx from developing and spreading themselves freely as they would otherwise do. The last petal, the *vexillum*, opposed to the ovarium at its upper suture, stands both from its situation as well as position,—as may be distinctly seen in numerous *Sophoreæ*,—furthest from the ovarium, consequently meets with the fewest hindrances to its independent development, and thus frequently attains to a considerable size in proportion to the other petals: this also depends on the stronger nutriment, which in consequence of its distance from the ovarium appears to be conveyed to it through the calyx. Thus then in the bud at least the vexillum will be folded round the other petals and inclose them, whence arises the well-known vexilla-covering æstivation (*æstivatio vexillaris*) of the *Papilionaceæ*.

If the petals are very narrow, and the calycinal tube very long and narrow, they at times cohere through their whole length at their margins to a tube whose border exhibits five incisions which open according to the type of the papilionaceous flower, as in many *Trifolieæ*.

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If on the contrary the calycinal tube is very short and broad, and the calyx thus surrounds the other floral parts but very loosely—as in most of the *Sophoreæ*—then indeed the carina is formed of two non-cohering petals, nevertheless the papilionaceous flower is still easily recognizable. This case has also a similar action on the stamina, which are then likewise free or only cohering at their base.

The stamina, which in the *Papilionaceæ* are with few exceptions always to the number of ten, stand, as is well known, in *two circles* around the ovarium. These two circles, it is true, are in most cases, from the cohesion of the filaments, very indistinct; yet in the young bud, as also in the perfectly developed flower of some *Sophoreæ*, they are clearly to be distinguished; and they are likewise indicated in numerous other *Papilionaceæ* by the alternate similar or sterile anthers (in this case it is constantly the inner circle which is sterile), and also by the alternately longer and shorter filaments. The stamina present but a very slight surface of opposition to the outer pressure, and on that account are subject to the most varied cohesions—the more so as they are situated nearest to the ovarium; nevertheless they are always more or less free at the apex, and I am only acquainted with a few cases where the anthers are directly sessile on the staminal tube.

Hitherto the following modifications of cohesion of the stamina have been observed:—

a. The stamina cohere in a perfectly closed tube.

b. The stamina cohere in a tube slit at the upper side, either in its entire length or only partially.

Here two cases are possible:

α. The staminal tube is slit from the apex downwards.

β. The staminal tube is slit from the base upwards. This is the rarer case.

c. The stamina cohere in a tube slit at the lower side along its whole length. Very rarely.

d. Nine stamina cohere to a tube slit superiorly; the tenth, belonging to the inner staminal circle, and standing opposed to the ovarium, is in its entire length free.

e. The stamina cohere in two bundles of 5 and 5 through-

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out their whole length; and as these two bundles stand on each side of the ovarium, they must be imagined to have originated from a staminal tube slit superiorly and inferiorly at the same time.

f. Of the ten stamina, *that* standing at the upper and *that* standing at the lower floral pole are free in their whole length (the first belongs to the second or inner, the latter to the first or outer circle); the other 8 stamina are situated in bundles of 4 and 4 on each side of the ovarium. (This case has hitherto been observed only in *Platypodium*, See 'Linnæa,' vol. xii. p. 420.)

Besides these, the stamina at times cohere more or less with the petals. The case most frequently occurring is the cohesion of nine stamina to a superiorly slit tube with a tenth free filament, and is to be explained thus: the tenth stamen, opposed to the suture of the pod, stands furthest from the ovarium, and is consequently the least subjected to pressure and the cohesion arising therefrom. That this is actually the case is moreover evident from the stamina situated superiorly on both sides of the ovarium entering successively into a more and more intimate cohesion towards the inferior floral pole, so that the stamina following on each side the free stamina, which belong to the outer circle, are frequently but slightly connected with the rest, while the succeeding ones cohere higher and higher,—a statement, which will be found to be confirmed in the greater number of diadelphic *Papilionaceæ*.

The other cohesions above-mentioned must also be explained in the same manner, from the general or partial, greater or smaller pressure which the stamina have to suffer from the adjacent floral parts; and there consequently exists no reason, as is also evident from the above-mentioned valuable researches of Schleiden and Vogel, for denying to the merely *mechanical* influences all action on the form and position of vegetable organs, as many botanists have done who have endeavoured to reduce all phænomena of vegetative life to the influence of higher influences, which unfortunately in most cases approaches near to scientific mysticism, by which little good is gained.

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Besides these, the stamina at times cohere more or less with the petals. The case most frequently occurring is the cohesion of nine stamina to a superiorly slit tube with a tenth free filament, and is to be explained thus: the tenth stamen, opposed to the suture of the pod, stands furthest from the ovarium, and is consequently the least subjected to pressure and the cohesion arising therefrom. That this is actually the case is moreover evident from the stamina situated superiorly on both sides of the ovarium entering successively into a more and more intimate cohesion towards the inferior floral pole, so that the stamina following on each side the free stamina, which belong to the outer circle, are frequently but slightly connected with the rest, while the succeeding ones cohere higher and higher,—a statement, which will be found to be confirmed in the greater number of diadelphic *Papilionaceæ*.

The other cohesions above-mentioned must also be explained in the same manner, from the general or partial, greater or smaller pressure which the stamina have to suffer from the adjacent floral parts; and there consequently exists no reason, as is also evident from the above-mentioned valuable researches of Schleiden and Vogel, for denying to the merely *mechanical* influences all action on the form and position of vegetable organs, as many botanists have done who have endeavoured to reduce all phænomena of vegetative life to the influence of higher influences, which unfortunately in most cases approaches near to scientific mysticism, by which little good is gained.

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Yet as there is no rule without at least an apparent exception, there may be persons who can bring forward a number of facts which appear to speak against the correctness of the theory here advanced; but these exceptions serve, as far as I have hitherto become acquainted with them, only to confirm and extend the above positions, which I only maintain for the true *Papilionaceæ* sufficiently well characterized by their *æstivatio vexillaris*.

One might mention, for instance, the large groups of the *Cæsalpineæ* and *Mimoseæ*, which can scarcely be separated from the family of the *Leguminosæ*, in which the almost regular five petalled corolla now and then occurs together with the characteristic pod, as not being in harmony with the law above stated for the *Papilionaceæ*, although the forms of flower which here occur are nothing more than modifications produced by that law.

The *Cæsalpineæ* are distinguished in addition to the erect embryo, which is of no importance in our inquiries, from the *Papilionaceæ* by the imbricate, the *Mimoseæ* by the valvate, æstivation.

The former appears to be produced by the calyx in the *Cæsalpineæ* being generally quinquepartite to the base; it is therefore not able to inclose the floral parts so tightly and to press them on one another, as a gamosepalous calyx; the petals can consequently develope more freely and adopt that æstivation originally peculiar to them.

In this case almost all the petals are of like size and form; they expand freely, not being prevented by the calyx, and approach in their outer appearance more to the rosaceous corolla than to the papilionaceous: the stamina likewise rarely cohere *inter se*, and we here find them arranged in two circles. If on the contrary the calyx is cohering (*Coulteria*, Hb. B. Kunth, *Cæsalpinia*, L., &c.) we immediately find the papilionaceous corolla make its appearance.

Further, when the ovarium in the *Cæsalpineæ* is spherical or cylindrical, then it will be less eccentric than the usually occurring compressed ovarium; its axis will approach nearer to the imaginary floral axis than is otherwise the case, for it

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If lastly the calyx is indeed gamosepalous tubular, but if the petals are provided with claws which exceed the calycinal tube in length, or if they cohere with it in their whole length, both which cases are of frequent occurrence in the *Mimoseæ*, then all reason for irregularity of the corolla disappears of itself, the corolla as well as the calyx are regularly quinquepartite or expanded rosaceously, and since the petals are then constantly acuminate, they can no longer cover one another laterally in the bud, but are merely folded valvately (*æstivatio valvata*). The stamina here frequently occur in very considerable number, and then, in consequence of the increased pressure by the inferiorly narrow calycinal tube, frequently cohere *inter se*, although above the tube they are perfectly free. At the same time the calycinal tube is here so narrow that there can no longer be a question as to a sensible eccentricity of the ovarium; and the influence which this would exert on the form of the corolla seems to be thus suspended, from the ovarium being frequently provided with a considerably long stipes, which appears to destroy the reaction against the unilateral pressure of the calyx, since it is but feeble. In this group we find the case, already frequently mentioned, of a pentagynous leguminous plant, which we have considered of such importance in explanation of the papilionaceous flower.

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EXPLANATION OF THE FIGURES.

Fig. 1. Diagram according to which the papilionaceous flower is constructed as regards disposition, and which actually occurs in *Affonsea*, St. Hil.

a, a, a, a. The abortive ovaries in the papilionaceous flower, *a'* the remaining ovarium.

b, b, b, b. Second inner staminal circle alternating with the ovarium.

c, c, c, c. Second outer staminal circle opposed to the ovaries.

d, d, d, d. Petals alternating with the ovaries.

e, e, e, e. Sepals opposed to the ovaries.

f. Imaginary floral axis.

Fig. 2. Diagram according to which the papilionaceous flower is actually constructed. Similar to the former, but the abortive ovaries *a, a, a, a,* are omitted.

Fig. 3. Diagram of a diadelphous papilionaceous flower.

a. Ovarium.

b. The tenth free stamen belonging to the inner circle.

c. The superiorly slit tube formed of the other nine stamens.

d'' d''. The two petals cohering at their inferior margin forming the carina.

d' d'. The two wings; *d.* the vexilla.

e, e, e, e. Sections of the calyx.

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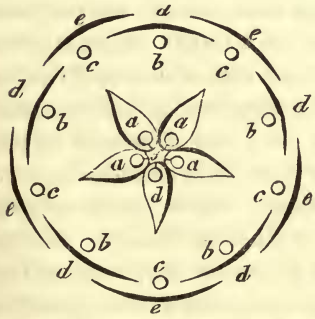
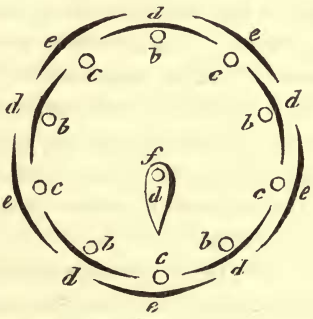


Fig. 2.



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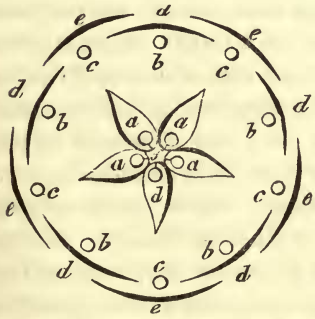

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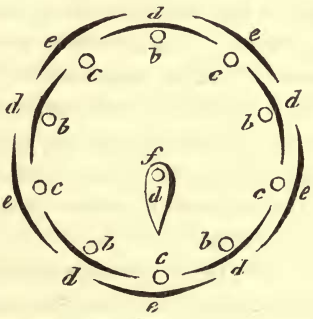

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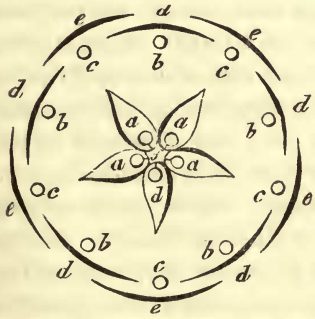

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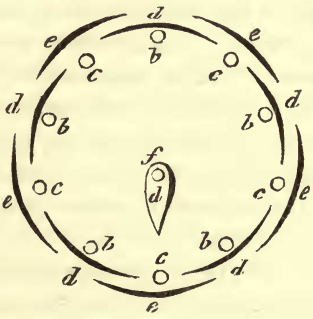

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